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PROVENANCE OF THE RED-BELLIED SNAKE, *STORERIA OCCIPITOMACULATA* (STORER) (SQUAMATA: NATRICIDAE), COLLECTED FROM EASTERN NEBRASKA, U.S.A., IN THE 19TH CENTURY

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ABSTRACT. I reaffirmed the existence of a red-bellied snake, *Storeria occipitomaculata* (Storer, 1839), collected in an allopatric locality in eastern Nebraska, U.S.A., in the 19th century. I utilized data associated with this snake, MCZ Herpetology R-135 (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts), to determine it was probably collected in the 1850s, approximately 170 years ago, either in the eastern portion of the Platte River Valley in western Douglas County or in the Missouri River Valley in eastern Washington County, bordering Iowa. I used this information to discuss the biogeographic and conservation implications for populations of *S. occipitomaculata* occurring in the Prairie Peninsula of the American Midwest and in the grassland-dominated plains. Moreover, I demonstrate the importance of reevaluating historic specimens in collections and the data associated with them to generate critical insights into species biogeography, ecology, and conservation.

KEY WORDS: biogeography; distribution; historical; Nebraska; Squamata; *Storeria occipitomaculata*

INTRODUCTION

Storeria occipitomaculata (Storer, 1839), the red-bellied snake, is a small (210–270 mm average total length [TL], 406 mm maximum TL), terrestrial natricid snake, generally distributed across much of eastern North America from Nova Scotia west to southeastern Saskatchewan, Canada, south to central Florida and the Gulf Coastal region, and west to eastern regions of Texas, Oklahoma, Kansas, and the Dakotas, U.S.A. (Trapido, 1944; Ernst, 2002; Ernst and Ernst, 2003; Powell et al., 2016; Pyron et al., 2016). Western disjunct populations exist in the Black Hills of South Dakota and adjacent Wyoming; Phillips County, north-central Kansas; and the Sierra Madre Oriental of Mexico (Taylor, 1942; Trapido, 1944; Fishbeck and Underhill, 1959; Smith, 1963; Ballinger et al., 2000; Collins et al., 2015; Pyron et al., 2016; Kiesow and Davis, 2020). The Mexican populations are often

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given full species status: *Storeria hidalgoensis* Taylor, 1942 (Ernst, 2008; Wallach et al., 2014; Boundy, 2021). More recently, a disjunct population of *S. occipitomaculata* was discovered along the Great Bend Reach of the Platte River Valley in Dawson, Buffalo, Phelps, Hall, and Kearney counties, south-central Nebraska (Peyton, 1989; Ballinger and Beachly, 1999; Ballinger et al., 2010; Fogell, 2010; Geluso and Harner, 2011, 2013; Harner and Geluso, 2011; Geluso, 2012; Tye et al., 2017).

Taylor (1891, 1892) and Hudson (1942) were unaware of the existence of any *S. occipitomaculata* in Nebraska, but in their compendia on Nebraska herpetofauna, each suggested it was an extralimital species that eventually could be discovered in this state (Taylor, 1891; Hudson, 1942). Trapido (1944) was the first to mention a disjunct *S. occipitomaculata* specimen, "MCZ 135," from Nebraska, but he did not depict it on his map. Wright and Wright (1952) note this species in Nebraska in their lists, without comment. Since then, a number of authors have consistently mapped this 19th century specimen, sometimes with doubt, along the Missouri River, the eastern border of Douglas County, Nebraska (Conant, 1958, 1975; Stebbins, 1966, 1985; Lynch, 1985; Conant and Collins, 1991; Ballinger et al., 2010; Powell et al., 2016). However, others have not depicted this individual on their distribution maps (Conant and Collins, 1998; Ernst, 2002; Ernst and Ernst, 2003; Stebbins, 2003; Pyron et al., 2016; Stebbins and McGinnis, 2018), and Fogell (2010) claims no vouchers exist from eastern Nebraska.

In this study I reaffirm the existence and provenance of this specimen of *S. occipitomaculata*, providing several potential collection localities. I use this information to discuss its biogeographic importance and relevance to conservation of this species in Midwestern and Plains populations.

MATERIALS AND METHODS

I used MCZ Herpetology R-135 (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts) to verify the existence and provenance of a specimen of *S. occipitomaculata* collected in the approximate area of contemporary eastern Nebraska. Catalog ledger data and contemporary mapping data posted on the Museum of Comparative Zoology online database (President and Fellows of Harvard College, 2022) was used to determine two nearly adjacent, potential collecting sites for this single specimen. An alternative interpretation of information in this catalog ledger, along with U.S. Army Corps of Engineers (2011) river navigation charts, were used to determine two other potential, adjacent collecting sites for this snake. Additionally, I used historic place names provided by the original collector (Hull) for MCZ R-135 along with two other specimens from Nebraska, both snakes, he deposited in the collection (MCZ R-134 and MCZ R-49) (President and Fellows of Harvard College, 2022), to provide further evidence for collection locality coordinates and an approximate range of collection years for MCZ R-135.

Additionally, I obtained geographic distances and coordinates through Google Earth (Google LLC, 2021). Interpreting historic, incomplete data necessitated rough approximations for determining distances and coordinates.

RESULTS

MCZ Herpetology R-135 is an adult male *S. occipitomaculata* (verified by Joseph Martinez, Acting Collection Manager/Curatorial Associate, MCZ Department of Herpetology) (264 mm approximate TL) with a metal tag embossed "135" (Fig. 1). Some key scalation features include: 15 middorsal scale rows, 124 ventral scales, a divided cloacal

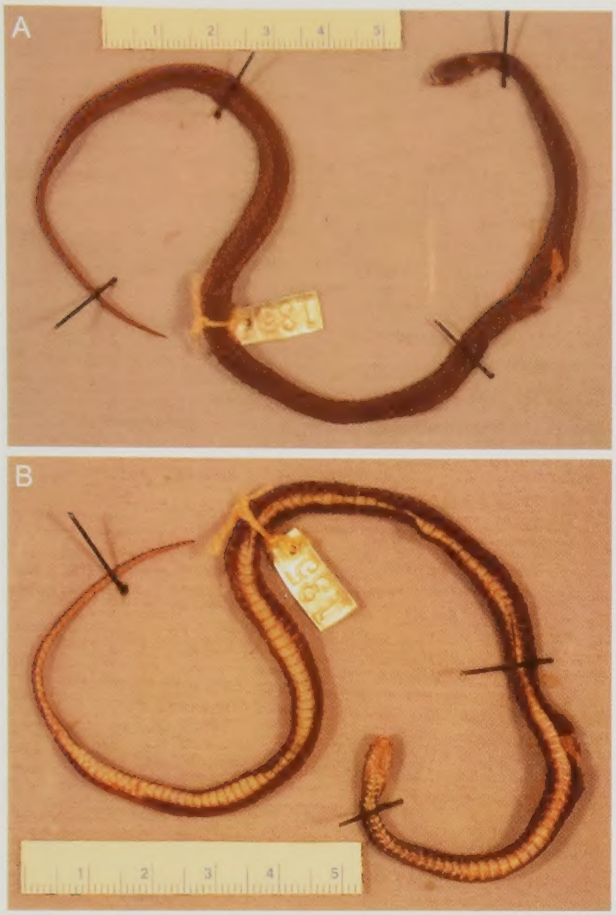


Figure 1. Dorsal (A) and ventral (B) views of MCZ Herpetology R-135, *Storeria occipitomaculata*, from eastern Nebraska (scale in cm). Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College, 2021. Photographs by Joseph Martinez.

scale, 51 divided subcaudal scales, 2 preoculars, and 6 supralabials (Figs. 1, 2). Three pale spots occupy the occipitonuchal region; the two lateral spots are paler than the central spot (Figs. 1, 2). Extensive morphological variation, especially in color and pattern, across the broad range of this species exhibits no significant geographic or genetic correlates and precludes any effort to use morphology to determine geographic affinities of this specimen (Ernst, 1974; Rossman and Erwin, 1980; Grudzien and Owens, 1991; Pyron et al., 2016).

The original catalog ledger book indicates it was collected in "[Nebraska]„ , 80 M.

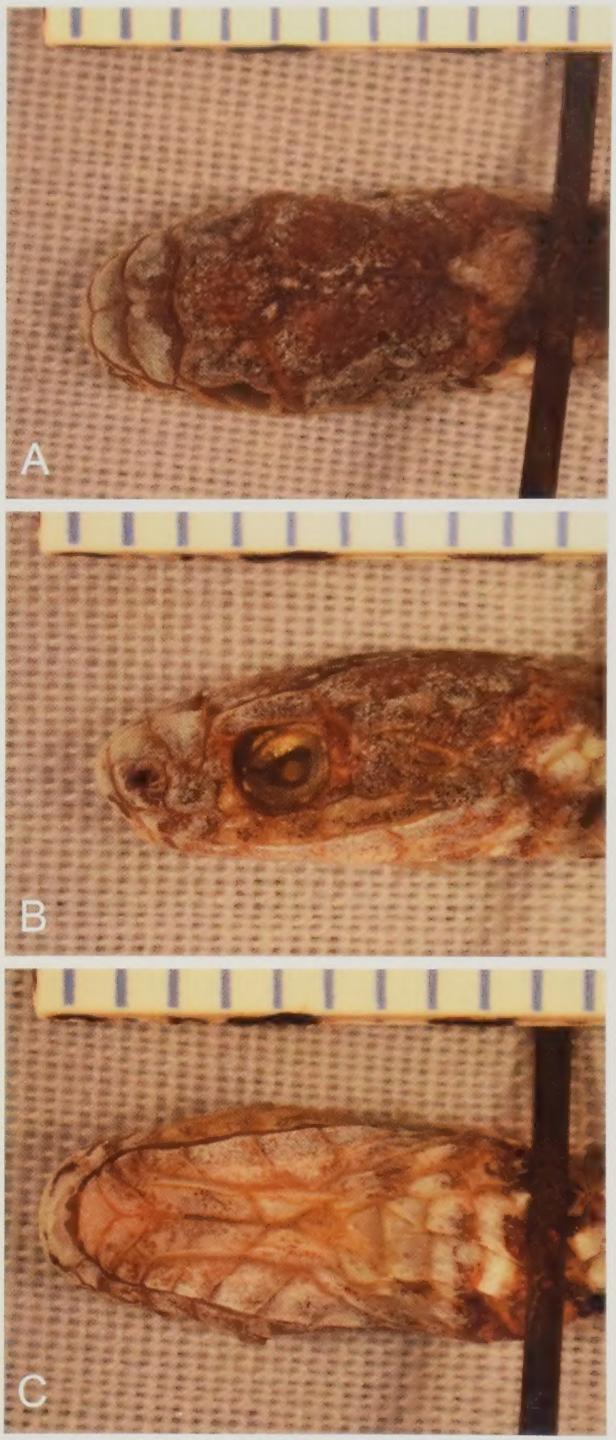
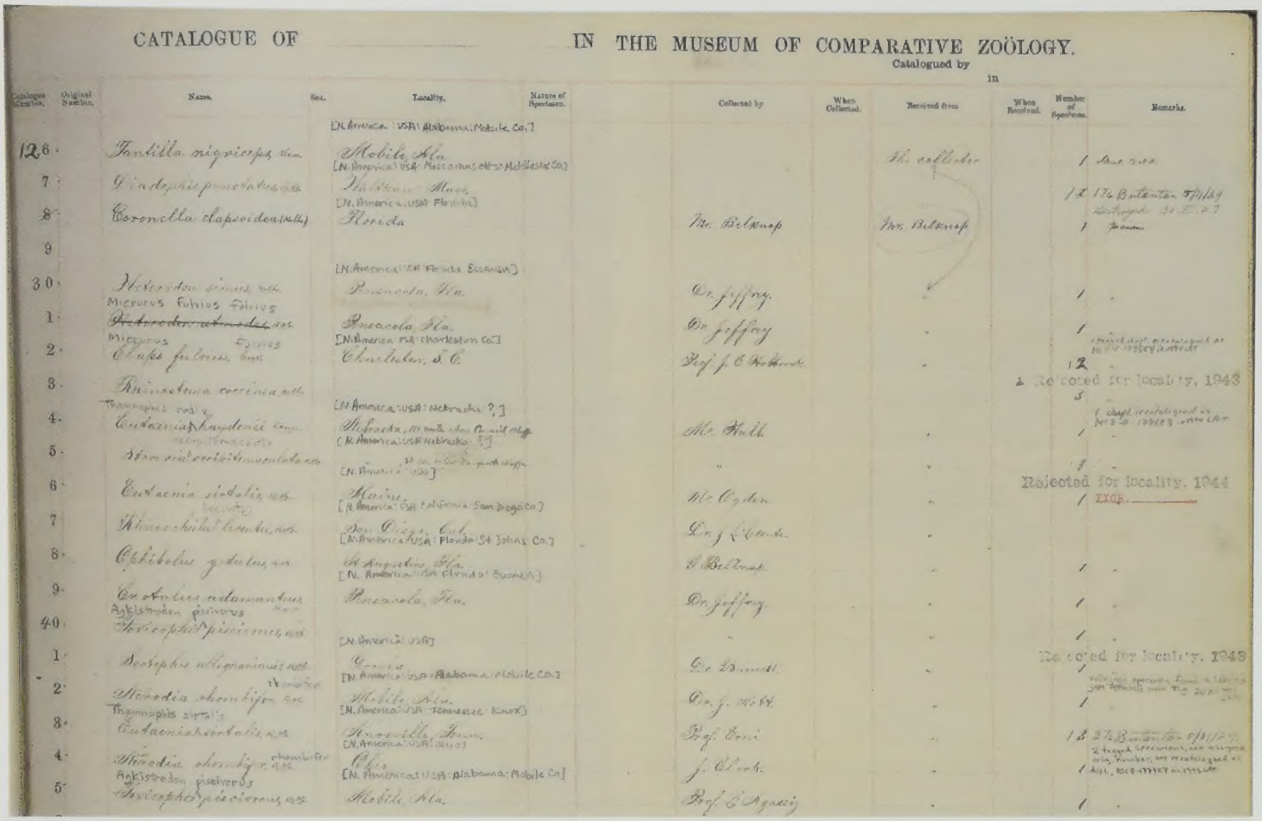


Figure 2. Dorsal (A), lateral (B), and ventral (C) views of the head of MCZ Herpetology R-135, *Storeria occipitomaculata*, from eastern Nebraska (scale in mm). Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College, 2021. Photographs by Joseph Martinez.


CATALOGUE OF _____ IN THE MUSEUM OF COMPARATIVE ZOÖLOGY.

Catalogued by _____ in _____

Catalogue Number.	Original Number.	Name.	Sex.	Locality.	Nature of Specimen.	Collected by	When Collected.	Received from	When Received.	Number of Specimens.	Remarks.
				[N. America: USA: Alabama: Mobile Co.]							
126		Tantilla nigriceps		Mobile, Ala.				H. collector		1	
7		Diadophis punctatus		[N. America: USA: Massachusetts: Middlesex Co.]						12	
8		Coronella elapsoides		[N. America: USA: Florida] Florida		Mr. Belknap		Mr. Belknap		1	
9											
30		Heterodon simus		[N. America: USA: Florida: Escambia] Pensacola, Fla.		Dr. Jeffrey				1	
1		Micrurus fulvius, Fabius									
2		Heterodon atmodes		Pensacola, Fla.		Dr. Jeffrey				1	
		Micrurus fulvius		[N. America: USA: Charleston Co.]							
		Elaps fulvius		Charleston, S. C.		Prof. J. E. Holbrook				12	
3		Rhinostoma coccinea								2	Rejected for locality, 1948
		Tropidonotus rigens		[N. America: USA: Nebraska ?]						5	
4		Eutaenia Kirtlandii		Nebraska, 10 miles above Council Bluffs		Mr. Hull				1	
				[N. America: USA: Nebraska ?]							
5		Storeria occipitomaculata		[N. America: USA]						1	
6		Eutaenia radalis		Maine		Mr. Ogden				1	Rejected for locality, 1944
7		Rhinochilus leconteii		[N. America: USA: California: San Diego Co.]							Exch.
8		Ophibolus getulus		Fort Diego, Cal.		Dr. J. Cooper					
				[N. America: USA: Florida: St. Johns Co.]							
9		Coluber obsoletus		St. Augustine, Fla.		S. Bellamy				1	
				[N. America: USA: Florida: Escambia]							
40		Coluber flagellum		Pensacola, Fla.		Dr. Jeffrey				1	
		Agkistrodon piscivorus									
1		Scytale coccinea		[N. America: USA]						1	
				[N. America: USA: Alabama: Mobile Co.]		Dr. Bennett				1	Rejected for locality, 1948
2		Storeria occipitomaculata		Mobile, Ala.		Dr. J. Wyatt				1	
		Thamnophis sirtalis		[N. America: USA: Tennessee: Knox]							
3		Eutaenia sirtalis		Knoxville, Tenn.		Prof. Troost				1	
				[N. America: USA: Illinois]							
4		Storeria occipitomaculata		Ohio		J. Clark				1	
		Agkistrodon piscivorus		[N. America: USA: Alabama: Mobile Co.]							
5		Coluber flagellum		Mobile, Ala.		Prof. L. Agassiz				1	

Figure 3. Portion of original ledger page of Catalog of Reptiles MCZ Herpetology. Data entered for MCZ Herpetology R-135, *Storeria occipitomaculata*, is on the 10th line. Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College, 2022.

below Sargents Bluff" by "Mr. Hull," likely entered in Samuel Garman's handwriting, with penciled-in annotations added by Joseph Martinez in the 1990s (Fig. 3; J. Martinez, personal communication). The "„" character is ditto for Nebraska and "M." is an abbreviation for miles, as seen in the line immediately above it for the locality of MCZ R-134, also collected by Hull (Fig. 3). The distance provided is approximately 128.75 km. No collection dates are entered for this or any of Hull's other specimens in MCZ Herpetology.

Sergeant Bluff (current correct spelling), in Woodbury County, Iowa, monickered before 1853 and immediately to the southeast of what was to become Sioux City, was named after Sergeant Charles Floyd of the Lewis and Clark *Corps of Discovery*, who died at what was to be called Sergeant Floyd's Bluff, or Floyd's Bluff, in 1804 (Coues, 1893; Thwaites, 1904–1905; Zimmerman et al., 1978). Sioux City, Iowa, which was not founded until 1855 (Zimmerman et al., 1978; Savage, 2007), currently surrounds the historic site of Floyd's Bluff and is now a metropolis adjacent to the city named Sergeant Bluff. Floyd's Bluff is approximately 7.40 km north–northwest of contemporary Sergeant Bluff. It is unclear whether Hull was referring to Floyd's Bluff or Sergeant Bluff. In 2005, Scott Hoy (University of Kansas Natural History Museum [KUNHM]) used U.S. Geological Survey map Bennett Reservoir East 41103-C5-TF 024 (1:24,000) to map this locality as 80 air miles south of Sergeant Bluff (President and Fellows of Harvard College, 2022), thus placing the collection

locality at 41°18′13″N, 96°22′41″W, which likely assumes Hull used latitude degrees in the 19th century to calculate north–south miles. If correct, this snake was collected near or on the east bank of the south-flowing section of the Platte River, west of the Elkhorn River before its confluence with the Platte and not far from the contemporary town of Valley, Nebraska (established in 1864; Fitzpatrick, 1925), near the western border of Douglas County (Fig. 4). However, if Floyd's Bluff is used as the place name reference, MCZ R-135 could have been collected approximately 7.40 km north–northwest of this site (41°21′14″N, 96°23′37″W), near contemporary I-275 but still within the Platte River Valley near the western edge of Douglas County (Fig. 4). These localities are approximately 175 km east of the nearest known population of this species in Hall County, in the Platte River Valley (Geluso and Harner, 2011, 2013).

Alternatively, Hull could have used the word "below" as a common colloquial synonym to refer to downstream. If so, then river miles were used as a unit of measure from either Floyd's Bluff or Sergeant Bluff, and the *S. occipitomaculata* would have been collected in the Missouri River Valley near a portion of the river broadly between the California Chute (41°34′15″N, 96°4′58″W) and Desoto Cut-off (41°31′0″N, 96°3′29″W) (U.S. Army Corps of Engineers, 2011; Fig. 4). This section of the Missouri River is bordered by Washington County, Nebraska (immediately north of Douglas County), on its western bank, adjacent to and including the contemporary city of Blair (established 1869: Fitzpatrick, 1925), and Harrison County, Iowa, on its eastern bank (U.S. Army Corps of Engineers, 2011), which places the specimen approximately 108 km south of the nearest population of *S. occipitomaculata* in Sioux County, northwestern Iowa

Figure 4. Map of potential collecting sites in eastern Nebraska for MCZ Herpetology R-135, *Storeria occipitomaculata*, represented by black stars. Contemporary city centers are represented by black rectangles and nonextant, historically inhabited area by a red rectangle. Thin black lines point to named geographic features on the Missouri River. Image by Louis A. Somma.

(Christiansen and Bailey, 1990; LeClere, 2013), 204 km east of the population in Hall County, Nebraska (Geluso and Harner, 2011, 2013), and 229 km north of populations in Atchison County, northeastern Kansas (Collins et al., 2015).

A variety of trading routes, immigrations, and expeditions passed directly through the above potential collecting localities before and during the 19th century railroad surveys (James, 1823; Jensen, 1975; Zimmerman et al., 1978; Moore, 1986; Pepperl and Bozell, 2018), but I could not determine the identity or profession of Mr. Hull, nor his activities while he was in the general area of eastern Nebraska.

Hull's place names for Nebraska collection localities of other specimens include: "Nebraska, 100 Miles above Council Bluff"

for a *Thamnophis radix* (Baird and Girard, 1853) ("*Eutaenia haydenii*, Kenn.": MCZ R-134) and "Nebraska, 15 miles North of Council Bluff" for a *Pantherophis ramspotti* Crother, White, Savage, Eckstut, Graham, and Gardner, 2011 ("*Scotophis vulpinus*, B. *et* G.": MCZ R-49). A duplicate (second *T. radix* specimen) with MCZ R-134 was listed in another ledger by L. A. Thomas in 1994 as MCZ R-178683, with Council Bluff written as "Council Bluffs" (President and Fellows of Harvard College, 2022).

The historic locale called Council Bluff in Nebraska, sometimes spelled Council Bluffs, was a place where indigenous peoples would gather to meet with Europeans and Euroamericans (James, 1823; Coues, 1893; Thwaites, 1904–1905; Jensen, 1975; Woodman, 2010; Pepperl et al., 2018; Pepperl and Bozell, 2018). It was located not far from what is now contemporary Fort Calhoun (established 1858 at the previous site of Fort Atkinson, which existed from 1820 to 1827: Fitzpatrick, 1925; Pepperl and Bozell, 2018; Pepperl et al., 2018), Washington County, Nebraska (Fig. 4). Council Bluff, Nebraska, is no longer extant and should not be confused with contemporary Council Bluffs, Pottawattamie County, Iowa (incorporated 1853: Savage, 2007), on the east bank of the Missouri River, opposite Omaha, Nebraska (established 1854: Fitzpatrick, 1925; Fig. 4).

None of Hull's place names for his Nebraskan collection localities refer to more obvious, populous contemporary cities established any time after 1852, such as Blair, Valley, Fort Calhoun and Omaha, Nebraska, and Sioux City and Council Bluffs, Iowa. Thus, MCZ R-135 was probably collected before 1853, at least 170 years ago, before Nebraska obtained official territorial status in 1854 (Fitzpatrick, 1925).

DISCUSSION

The specimen of *S. occipitomaculata* MCZ R-135, collected in eastern Nebraska in the mid-19th century, likely was collected at one of two general localities: either in the Platte River Valley, near Valley, western Douglas County, Nebraska, or in the Missouri River Valley, near or within Blair, Washington County, Nebraska, or perhaps the western border of Harrison County, Iowa. Both of these localities are allopatric from other populations of red-bellied snakes in all coordinate directions.

If MCZ R-135 was collected in the Platte River Valley in Douglas County, it could represent an eastern extension and, perhaps, continuation of this species from the Great Bend Reach of the Platte River Valley in south-central Nebraska (Ballinger et al., 2010; Fogell, 2010; Geluso and Harner, 2011, 2013; Geluso, 2012). If this specimen was collected in the Missouri River Valley, Washington County, Nebraska, or even Harrison County, Iowa, it could represent an undetected population or populations of red-bellied snakes filling a gap in the species' distribution between eastern Kansas to the south and eastern South Dakota and northwestern Iowa to the north (Christiansen and Bailey, 1990; Ballinger et al., 2000; LeClere, 2013; Collins et al., 2015; Davis et al., 2017; Kiesow and Davis, 2020). Intensive collecting in either of these two likely localities may reveal a previously undetected distributional connection between western populations of *S. occipitomaculata* in south-central Nebraska and populations eastward in Iowa (Ballinger and Beachly, 1999; Ballinger et al., 2010), if not simply more disjunct populations.

Storeria occipitomaculata is a secretive, usually nocturnal, terrestrial snake dependent on mesic, relatively undisturbed environments throughout its range, but it is often tolerant of suburban and rural anthropo-

genic habitat and is not limited to forested ecosystems (Over, 1923; Ernst and Ernst, 2003; Harner and Geluso, 2011; Brown and Phillips, 2012; Dieter and Ronningen, 2017; Kiesow and Davis, 2020). Populations in south-central Nebraska are at least tolerant of and may benefit from pasture burning (Harner and Geluso, 2011). The red-bellied snake's diet of soft-bodied invertebrates includes anatomical and behavioral specializations for capturing and ingesting terrestrial gastropods that are shared by other members of the genus *Storeria* (Rossman and Myer, 1990; do Amaral, 1999). This dietary specialization could further limit its distribution to mesic environments favored by their prey.

Red-bellied snakes were once thought excluded from the post-Pleistocene Prairie Peninsula in parts of the American Midwest by xeric conditions (Schmidt cited in Trapido, 1944). This provided further evidence for Schmidt's (1938) hypothesis regarding the effects of the Prairie Peninsula on the distribution of North American herpetofauna. This interpretation, however, is complicated by several incompletely understood prairie expansion and contraction events occurring at different times after the Pleistocene (Kopera, 2019; Blais et al., 2021). Populations of highly cold tolerant biota, including *S. occipitomaculata* and their prey, could have existed, some as relicts, along glacial margins and tundra during the Pleistocene, allowing them to recolonize the Prairie Peninsula readily during glacial retreats (Brown and Phillips, 2012; Blais et al., 2021). Moreover, a recent assessment of the distribution of *S. occipitomaculata* in Illinois indicates that, in addition to inhabiting wooded ecosystems, this species occurs statewide in a variety of grassland and unforested habitats, including those altered through anthropogenic use, and is only excluded from active croplands (Brown and Phillips, 2012). Christiansen and Bailey (1990) previously had indicated that the distribution of *S. occipitomaculata* in Iowa was limited to the eastern and northern portions of the state, west to the northwestern corner, with no vouchers from central, southern, and most of the western portion of the state. More recently LeClere (2013) indicated additional vouchers for portions of southern, south-central, and central Iowa, with a reduced distributional hiatus in the southwestern and western portions of that state. Additionally, some Iowa populations occur in sandy, xeric habitat (LeClere, 2013). Presumably, suitable moist microhabitat allows populations of this semifossorial species and their prey to inhabit these areas. Further collecting in the Prairie Peninsula of Iowa may reveal previously undetected populations of *S. occipitomaculata* closer to eastern Nebraska, unless they are currently extirpated by agricultural degradation.

In Nebraska, suitable mesic environments for red-bellied snakes include riparian deciduous forests and lowland tallgrass prairies that historically characterized most major river valleys and bottomlands (Kaul et al., 2011). Relatively xeric environments cannot be ruled out if moist, likely subterranean microhabitats are available for these snakes and their prey. It is unclear whether MCZ R-135 represents a specimen from an extant population of *S. occipitomaculata* in eastern Nebraska with affinities to populations along the Platte River in the south-central region of the state; to eastern populations in Kansas, Iowa, and South Dakota; or to both. If undegraded mesic habitats exist in these regions, intensive collecting surveys may help delimit the red-bellied snake's occurrence and biogeographic affinities in Nebraska. Discovering new populations of *S. occipitomaculata* in eastern Nebraska, and perhaps along the east bank of the Missouri River bottoms in Iowa, might only be limited

by past extirpations caused by intensive anthropogenic habitat degradation—principally croplands.

Also possible is that MCZ R-135 represents an allopatric population, whether extant or currently extirpated. Disjunct populations characterize this species' distribution in western portions of its range and in grassland regions of the Midwestern Prairie Peninsula, some of which may represent relict populations from Pleistocene refugia and others corroborating post-Pleistocene reinvasions of deglaciated land (Smith, 1963; Brown and Phillips, 2012).

In Nebraska, red-bellied snakes are a Tier 1 at-risk species; State Imperiled (S2) (Schneider et al., 2018). Determining the status of this species in eastern Nebraska will further delimit its regional environmental requirements and help formulate conservation recommendations for other seemingly disjunct populations in the American Midwest and westward into the grassland-dominated plains.

Lastly, this study emphasizes the utility of reevaluating historic specimens in collections. Despite vague and, perhaps, lost data associated with them, they can still provide invaluable sources for assessing past information and generating new insights critical to studies on biogeography, ecology, and conservation.

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